Pedobiologia **30**, 285—298 (1987)
VEB Gustav Fischer Verlag Jena

Department of Environmental and Forest Biology,
State University of New York, College of Environmental Science
and Forestry, Syracuse, New York, USA

Functional ecology of coprophagous insects: A review

BRUCE G. STEVENSON and DANIEL L. DINDAL

With 4 figures

(Accepted: 87-02-25)

1. Introduction

Traditionally, ecologists have viewed ecosystem properties in the contexts of energy flow and nutrient cycles. Relatively recent scientific attention has focused on the role of consumers as regulators of ecosystem processes (CHEW 1974; KITCHELL *et al.* 1979), For example, detritivorous invertebrates participate in the decay of organic matter which releases nutrients for plant growth (ANDERSON *et al.* 1983). These organisms utilize relatively little of the energy they consume. A primary role of detritivores is the stimulation of the metabolism of microbes, which are responsible for most organic matter decomposition. PETERSEN & LUXTON (1982) and PARKINSON (1983) have extensively reviewed the functional ecology of soil invertebrates.

Coprophagous arthropods actively contribute to the degradation of fecal material, particularly ruminant dung. Most research on coprophagous arthropods has dealt with their beneficial activity in the maintenance and utilization of agricultural ecosystems (BORNEMISSZA 1960; FINCHER 1981). The purpose of this paper is to examine and review the roles of these organisms in the context of consumer regulation of organic matter decomposition. Since the majority of related research has focused on ruminant dung, this review will emphasize the role of invertebrates inhabiting it.

2. Properties of heterotrophic microcommunities

Heterotrophic microcommunities, such as dung, are characterized by negligible or nonexistent primary production (DINDAL 1973). Initial, maximal energy declines through decomposition. This decay usually is exponential since labile organic matter is utilized rapidly and recalcitrant fractions decompose more slowly (OLSON 1963; MINDERMAN 1968), although substrate complexity may modify these rates (BUNNELL *et al.* 1977; HUNT 1977). This decomposition produces unstable and ephemeral habitats for the large number of invertebrate and microbe species that inhabit them (DINDAL 1973; BEAVER 1977). Decomposition of ruminant dung usually is slow, due to the initial conditions of anaerobiosis and subsequent drying (STEVENSON & DINDAL 1987).

3. Coprophagous arthropods

Coprophagous athropods can be classified according to their behaviour within dung pats (BORNEMISSZA 1960; Table 1). Endocoprophages include those insects in which larval development takes place within the dung pat. This group involves all flies which breed in

Table 1. Classification of coprophagous arthropods based upon BORNEMISSZA (1969)

Classification	Development of larvae	Representative taxa
Endocoprophagous	Within dung pat	Diptera Muscidae Anthomyidae Coleoptera Scarabaeidae Aphodinae Hydrophilidae
Paracoprophagous	Within dung ball buried Beneath dung pat	Coleoptera Scarabaeidae Scarabaeinae Geotrupinae
Telecoprophagous	Within dung ball buried Away from dung pat	Coleoptera Scarabaeidae Scarabaeinae Geotrupinae

dung and beetles in the Hydrophilidae (larvae are predatory) and the Aphodinae of the Scarabaeidae. BORNEMISSZA (1969) reported that some scarabaeid species also breed in the dung pat. Para- and telecoprophages include beetles in which dung balls are constructed by the adults. Paracoprophages bury dung balls (each with one egg) directly beneath the dung pat and telecoprophages remove dung balls a distance away from the dung and then bury them. These groups involve species in the Geotrupinae and Scarabaeinae of the Scarabaeidae.

Although all coprophagous arthropods utilize dung as food, the ways in which they consume it differ. Adult scarabaeid beetles concentrate dung particles by pressing dung between labral and labial pads of setae (MADLE 1934; LANDIN 1961; HATA & EDMONDS 1983); these organisms digest microbiota and soluble organic matter. Larval beetles possess chewing mouthparts with which they consume dry dung. Cyclorraphous fly larvae sieve particles of dung between pharyngeal ridges (DOWDING 1967) and they probably depend upon microflora as a main food source (D'AMATO *et al.* 1980). MATTHIESEN *et al.* (1984) demonstrated that the size of emerging *Musca vetustissima* WALKER adults was reduced when dung was coarse and dry. This substrate was less nutritious than moist dung in which the microbial populations were available in the liquid portions of dung.

4. Role of invertebrates in organic matter decomposition

4.0. Prefatory note

The roles of invertebrates in heterotrophic microcommunities have been viewed in several ways. Generally, they are seen as regulators of the decomposition process (CROSSLEY 1977). Invertebrates may accelerate or delay nutrient release from organic matter in both direct and indirect ways (Table 2). The effects of coprophagous arthropods on the physical and biological properties of the dung habitat are shown in Fig. 1.

4.1. Direct effects of invertebrates

4.1.0. General remarks

The direct effects of detritivorous invertebrates in decomposition, which include consumption and burial of organic matter, have received considerable scientific attention (KOWAL & CROSSLEY 1971; MCBRAYER & REICHLE 1971; MACLEAN 1974; CORNABY *et al.* 1975). Newly dead organic matter usually is not available to detritivorous arthropods since they lack the ability to digest cellulose and other structural polysaccharides, although some detritivores possess endogeneous carbohydrases (e.g., OVERGAARD-NIELSEN 1962; HARTENSTEIN 1982). Instead most decomposition occurs through microbial metabolism.

Table 2. Summary of effects of detritivorous invertebrates on organic matter decomposition[1])

Interaction	Effect on decomposition	Representative References
Consumption of detritus	Metabolism of organic matter by invertebrates with carbohydrase enzymes	McBrayer & Reichle 1971; Cornaby *et al.* 1975
Burial of detritus	Mixture of detritus with underlying substrate	Dindal *et al.* 1979; MacQueen & Beirne 1975a
Fragmentation of detritus	Exposure of increased surface area of detritus to microbial metabolism	Edwards *et al.* 1970; Petersen & Luxton 1982
Aeration of detritus	Exposure of substrate to oxygen; promotion of aerobic decomposition	Edwards 1958; Edwards & Rolley 1965
Conversion of detritus to feces	Exposure of substrate to intestinal microflora Increased microbial metabolism	Crossley 1977; Webb 1977; Anderson & Ineson 1982
Grazing on microbes	Within certain densities, stimulation of microbial metabolism Prevention of mycostasis and bacteriostasis Increases in bacterial populations and reduction in fungal populations	Hanlon & Anderson 1980; Ineson *et al.* 1982
Stimulation of bacteriophagous nematode populations	Growth in bacterial populations Increased bacterial metabolism	Abrams & Mitchell 1980a, b; Anderson *et al.* 1983
Distribution of microbes to fresh detritus	Increased microbial populations and respiration	Parkinson *et al.* 1979; Hassal *et al.* 1983

[1]) See text for further explanation.

4.1.1. Consumption of Dung

In general, dung beetle larvae have high consumption rates (Myrcha 1973; Holter 1974, 1975; see Fig. 1). Holter (1974) suggested that rapid decomposition of dung, coupled with a low assimilation efficiency, accounted for the high ingestion rate of *Aphodius* larvae (endocoprophages). *Aphodius* larvae do not possess carbohydrase enzymes and thus cannot decompose structural polysaccharides (Holter 1974). Larvae of para- and telecoprophages, some of which possess intestinal flagellates capable of digesting cellulose, egest their feces along the inside walls of their brood balls. They consume their excreta several times during their development. Thus, the calorific value of dung in brood balls decreases with age (Myrcha 1973). These phenomena provide support for the "external rumen" concept (Mason & Odum 1969).

Since coprophagous fly larvae sieve particles in their feeding activity (including liquid portions of dung), estimation of consumption rates is difficult. An estimate of the feeding rate of *Paregle sp.* larvae (Anthomyiidae) was derived from Olechowicz (1976): 1.242 mg dung consumed/mg dry body mu/day. Coprophagous fly larvae probably consume too little organic matter to exert significant direct effects on dung degradation (see below).

In some desert and tropical grassland ecosystems, termites consume significant portions of ruminant dung and can account for 19.5 to 100% of mass loss (Omaliko 1981; Whitford *et al.* 1982, 1983).

4.1.2. Burial of dung

Forest soil macroinvertebrates bury organic matter and mix it with underlying soil. Earthworms are particularly important in this process, since they constitute up to 75% of the invertebrate biomass in some forest soils (Kühnelt 1976). They are also important in incorporation of municipal sewage sludge, slurries or sewage effluents into soil (Curry 1976; Dindal *et al.* 1979).

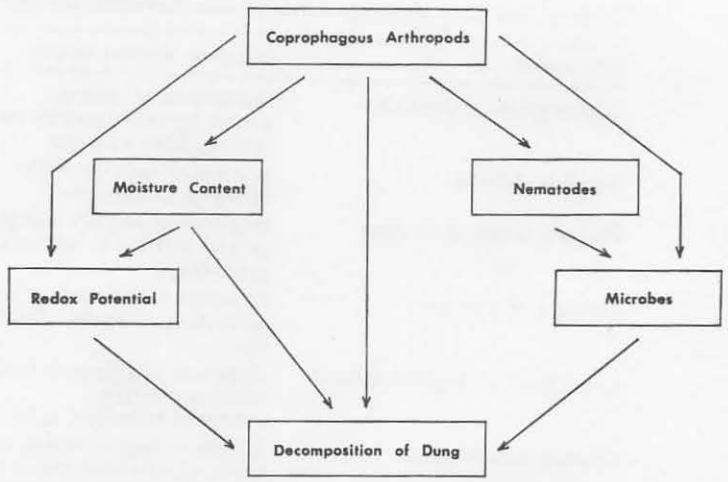

Fig. 1. Schematic representation of the effects of coprophagous arthropods on physical and biological properties of cow dung. Arthropods can promote decomposition directly through their consumption of dung and indirectly through their effects on moisture content, redox potential, microbial density and nematode population density. Arrows indicate direction of effect.

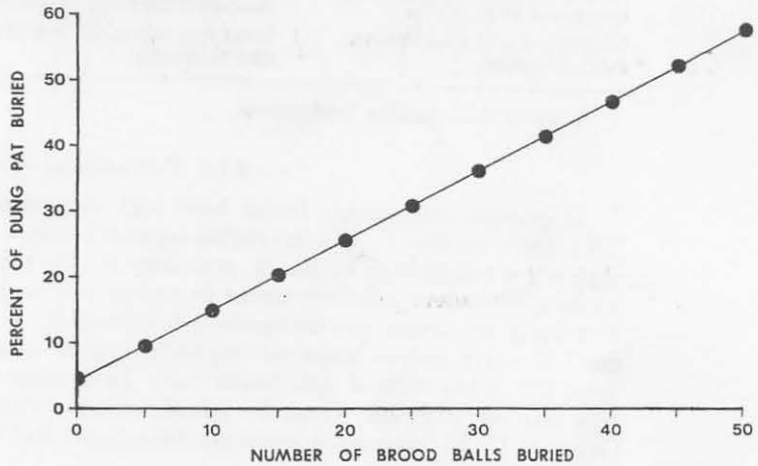

Fig. 2. Simulation of the effect of burial activity by *Onthophagus nuchicornis* (L.) (Scarabaeidae) adults on burial of cow dung. Regression equation taken from MacQueen & Beirne (1975a) ($Y = 1.08\,X + 4.14$; $n = 10$; $r = 0.96$; $p < 0.001$).

Burial of dung is an important process conducted by scarabaeid beetles. A number of researchers have indicated that the amount of dung buried by para- and telecoprophages in laboratory studies is a function of the population density of adult beetles (Fig. 2; Breymeyer 1974; MacQueen & Beirne 1975a; Ridsdill Smith *et al.* 1982; Kirk 1983). However, Hughes (1975) concluded that the amount of dung buried in the field is not directly related to beetle population density.

Adult *Aphodius spp.* mix large amounts of dung with underlying soil, even though they do not form and bury dung balls (Breymeyer 1974). Aphodine larvae also bury dung prior to pupation.

Rapid burial of dung can have several beneficial consequences from an agricultural point of view: (1) reduction in nitrogen loss as ammonia (Gillard 1967); (2) increased growth of

pasture plants (BORNEMISSZA & WILLIAMS 1970; FINCHER *et al.* 1981; WICKLOW *et al.* 1984); (**3**) destruction of helminth parasites of livestock (BRYAN 1973, 1976; FINCHER 1973, 1975; BERGSTROM *et al.* 1976; ENGLISH 1979); and (**4**) suppression of pestiferous fly populations (BORNEMISSZA 1970; BLUME *et al.* 1973; HUGHES *et al.* 1978; SMITH 1981; BLANK *et al.* 1983; FAY & DOUBE 1983; WALLACE & TYNDALEBISCOE 1983). The effects of these coprophages will, however, depend upon the distribution of dung within an agricultural system and the stocking density of domestic animals.

Burial of dung also can have other influences that are not related to agricultural production. For example, BERTRAND & LUMARET (1984) demonstrated that burial of sheep feces by scarabaeid beetles had a deleterious impact on microarthropod populations. The decline of microarthropods may indirectly cause decomposition to slow (see below).

4.2. Indirect effects of invertebrates

4.2.0. General

Detritivorous invertebrates which cannot assimilate fresh organic matter can contribute to the decomposition process in several indirect ways. These indirect effects may exceed their direct effects in some habitats (CROSSLEY 1977; PARKINSON 1983).

4.2.1. Fragmentation of dung

Invertebrates disintegrate plant and animal tissues and make them more easily leached and invaded by microorganisms. By fragmenting detritus, invertebrates increase the surface area available for microbial metabolism, which increases decomposition rates (MCBRAYER 1973; PETERSEN & LUXTON 1982). Moreover, microbes cannot attack some leaf species without preliminary fragmentation. If this physical destruction is experimentally retarded, litter decomposition is slowed (KURCHEVA 1960; VAN DER DRIFT & WITKAMP 1960; WITKAMP & CROSSLEY 1966; EDWARDS *et al.* 1970). Fragmentation of leaf litter in freshwater streams also is an important function of macroinvertebrates ("shredders") (CUMMINS *et al.* 1973; BENFIELD *et al.* 1977; SHORT & MASLIN 1977; ANDERSON *et al.* 1978; ANDERSON & SEDELL 1979; MULHOLLAND *et al.* 1985).

Coprophagous arthropods exert differential effects on dung fragmentation. Adult beetles and fly larvae, which have sucking mouthparts, lack the morphological adaptations to fragment dung. Larval dung beetles, which have chewing mouthparts, can crumble and disrupt a dung pat. LUSSENHOP *et al.* (1980) found that dung without insects or with only fly larvae was essentially intact over one month. Dung containing *Aphodius* larvae was crumbly in comparison. STEVENSON & DINDAL (1987) also found that aphodine larvae caused considerable fragmentation of dung.

4.2.2. Aeration of dung

In very moist heterotrophic substrates, burrowing macroinvertebrates can aerate the substrate and thus accelerate aerobic decomposition. Mixing of municipal sewage sludge with drier soil by earthworms increased the redox potential and oxygen availability in sludge (STEVENSON *et al.* 1984). Aeration stimulates the growth of aerobic microflora and enhances sludge decomposition. It also causes decreased density of pathogenic microorganisms (BROWN & MITCHELL 1981).

Similarly, turnover of sediment and detritus by aquatic macroinvertebrates increases the depth of oxygen penetration (and thereby, the depth of aerobic metabolism) (EDWARDS 1958; EDWARDS & ROLLEY 1965) and provides space for further microbial activity (HARGRAVE 1970, 1976). Feeding activity of large shredders loosens leaf packs in woodland streams (ANDERSON & SEDELL 1979) and thereby increases the availability of oxygen to the centers of the packs.

Little research has been reported to this point on the effects of coprophagous arthropods on oxygen availability and redox potential in dung. However, scarabaeids and fly larvae accelerate the rate of drying in dung (BRYAN 1973; ANDERSON & COE 1974; FERRAR 1975;

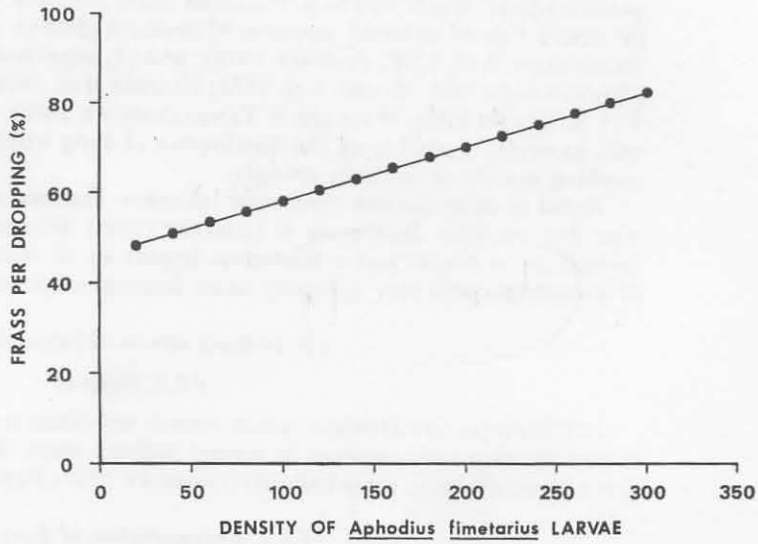

Fig. 3. Simulation of the density effect of *Aphodius fimetarius* (L.) (Scarabaeidae) larvae on conversion of cow dung to insect frass. Regression equation derived from MERRITT (1974) ($Y = 0.121 \times + 46.227$; $n = 16$; $r = 0.825$; $p < 0.01$).

MACQUEEN & BEIRNE 1975b; STEVENSON & DINDAL in press) and therefore, increase the aeration (LUSSENHOP *et al.* 1980; Fig. 1). STEVENSON & DINDAL (in press) reported significant increases in *Eh* with insect activity in cow dung.

4.2.3. Conversion of dung to invertebrate feces

Another important indirect role of detritivorous macroinvertebrates is the conversion of organic matter to invertebrate feces (PETERSEN & LUXTON 1982), which is a form of substrate modification (CROSSLEY 1977; WEBB 1977). Since most detritivorous invertebrates have low assimilation efficiencies, they egest much of the organic matter they consume and thus have been called "feces factories". Feces of litter-feeding invertebrates differ from the original substrate in several ways: feces are higher in *p*H, have greater moisture holding capacity and increased surface-to-volume ratios, and are more amenable to colonization by bacteria than fungi (MCBRAYER 1973; WEBB 1977). SATCHELL & MARTIN (1984) report elevated phosphatase activity in earthworm feces as compared to activity in soil.

Feces production by coprophagous invertebrates has been investigated in only a few studies. *Aphodius fimetarius* L. larvae convert a large portion of a dung pat to insect frass, depending upon their population density (Fig. 3; MERRITT 1974). STEVENSON (unpubl.) simulated energy flow in an *A. rufipes* (L.) larva and found that the larva consistently egested over 90% of the energy it consumed, although this value declined slightly with temperature. Thus, the dung beetle is a "feces factory". The pattern of decomposition of these feces is unknown.

4.2.4. Effects on coprophagous microflora

Interactions of invertebrates with microflora are probably the most important indirect roles of macroinvertebrates in organic matter decomposition (CROSSLEY 1977; PARKINSON 1983; WALLWORK 1983; SEASTEDT 1984). Arthropods consume large numbers of bacteria and fungi. Within certain arthropod densities, this predation stimulates microbial growth and metabolism and it prevents bacteriostasis and mycostasis (MACFADYEN 1961; HARGRAVE 1970, 1976; AUSMUS & WITKAMP 1973; STOUT 1973; MCBRAYER *et al.* 1974; VAN DER DRIFT & HANSEN 1977; BROWN *et al.* 1978; ANDERSON *et al.* 1978; ANDERSON & SEDELL

1979; PARKINSON *et al.* 1979; HANLON & ANDERSON 1980; INESON *et al.* 1982; ANDERSON & INESON 1983). NEWELL (1984) reports differential effects of grazing by a collembolan on the growth and metabolic activity of two decomposer basidiomycetes. Decomposition of litter also showed differential effects as a result.

HOLTER (1977, 1979b) found that feeding on dung by *Aphodius rufipes* larvae stimulated microbial respiration, since weight loss was nearly seven time greater than the amount which the larvae assimilated. NAKAMURA (1975) also reported accelerated mass loss of dung in the presence of scarab beetles.

Passage of organic matter through the guts of many detritivorous macroinvertebrates increases the populations of bacteria and actinomycetes and their metabolic activity since the guts of soil animals are more favorable environments for microbial growth than the external environment (PARLÉ 1963; WENT 1963; SZABÓ *et al.* 1969; HARGRAVE 1970, 1976; REYES & TIEDJE 1975; BAKER & BRADMAN 1976; STEFANIAK & SENICZAK 1976; BROWN *et al.* 1978; ANDERSON & BIGNELL 1979; HORNOR & MITCHELL 1981; ANDERSON & INESON 1983; CRAWFORD & TAYLOR 1984). Thus, feces have an elevated rate of microbial metabolism and lose mass more rapidly than uneaten detritus, although these phenomena are not universal (NICHOLSON *et al.* 1966).

Dung in the gut of *Scarabaeus spp.* larvae has bacterial populations which are two to three times more dense than those in uneaten dung (HALFFTER & MATTHEWS 1971). In *Chironitis spp.* the difference is 17 times. Thus, as in other detritivores, the gut of the scarab larva is a more favorable environment for bacterial growth.

Invertebrate grazing on microbial populations usually exerts differential effects on bacteria and fungi. HANLON & ANDERSON (1979) found that grazing by a collembolan, *Folsomia candida* WILLEM, increased bacterial and reduced fungal standing crops in proportion to grazing intensity. Feeding by *Glomeris marginata* (VILLERS) (Diplopoda) and *Oniscus asellus* (L.) (Isopoda) also suppressed fungal populations and enhanced bacterial activity (HANLON & ANDERSON 1980). With increasing litter fragmentation, bacterial populations increase (PARKINSON 1983).

ANDERSON & INESON (1983) demonstrated that feeding on litter by arthropods, such as millipedes and isopods, can stimulate microbial respiration. Beyond an optimal level, however, this feeding activity can inhibit microbial activity and is associated with decreased fungal and increased bacterial populations. Two factors appear to be responsible for these shifts: (**1**) disruption of hyphae which prevents or retards fungal growth (bacterial are not so affected) and (**2**) rapid growth of bacterial populations in the guts of macroinvertebrates. Microarthropods (e.g., Collembola), which feed selectively on fungi, also may have pronounced inhibitory effects when their populations densities are high.

Coprophagous arthropods exert similar effects. Dipteran and scarabaeid larvae decreased fungal biomass and increased bacterial populations in sheep and cattle dung (BREYMEYER *et al.* 1975; LUSSENHOP *et al.* 1980). Mixing of dung by these insects constantly exposes new substrate to bacteria while fungal hyphae are disrupted. Since fungal growth rates are generally less than those of bacteria, their populations are reduced (DICKINSON & UNDERHAY 1977; LUSSENHOP *et al.* 1980). WICKLOW & YOCUM (1982) reported that grazing by larval *Lycoriella mali* FITCH (Diptera: Sciaridae) caused a reduction of species richness of coprophilous fungi in rabbit dung.

The activity of scarabaeid and dipteran larvae stimulates ammonifying bacteria (BREYMEYER *et al.* 1975). Therefore, these arthropods may increase the production of ammonia from dung (MCKINNEY & MORLEY 1975). MACQUEEN & BEIRNE (1975b) demonstrated that increasing population density of *Musca domestica* (L.) caused small nitrogen losses from cattle dung (see Fig. 4). The population densities of fly larvae used in this study were greater than field densities of muscoid flies in dung. Exact effects of field populations of flies on nitrogen loss thus are unknown, but can be expected to be minimal.

Detritivorous invertebrates can also indirectly stimulate bacterial populations and metabolism through their effects on bacteriophagous nematodes (e.g., PARKER *et al.* 1984; see

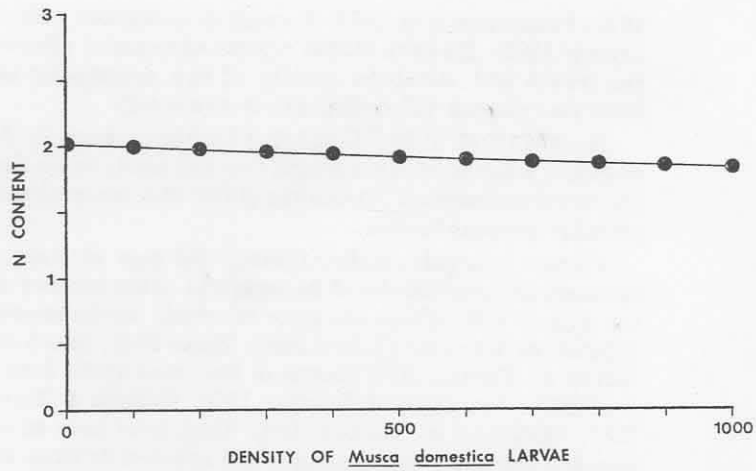

Fig. 4. Simulation of the density effect of *Musca domestica* (L.) (Diptera) larvae on the nitrogen content of cow dung. Regression equation taken from MacQueen & Beirne (1975 b) ($Y = 2.0221 - 0.0002\ X$; $n = 5$; $r = 0.95$; $p < 0.05$). Slope is not significantly different from zero.

Fig. 1). Feeding upon sewage sludge by *Eisenia fetida* (Savigny) (Oligochaeta) or *Oniscus asellus* increased population densities of bacteriophagous nematodes (Brown *et al.* 1978; Mitchell *et al.* 1978, 1980). Nematodes, in turn, stimulate bacterial growth and metabolism (Abrams & Mitchell 1980 a, 1980 b). Anderson *et al.* (1983) found that more nitrogen was mineralized from soil microcosms containing both bacteria and bacteriophagous nematodes than from those with bacteria alone. Parker *et al.* (1984) concluded that microinvertebrates, such as nematodes, may be important regulators of decomposition through their effects on bacteria. Additionally, protozoans feeding on bacteria increased microbial metabolism by increasing turnover rates of bacteria (Stout 1973; Fenchel & Harrison 1976).

Effects of coprophagous arthropods on bacteriophagous nematodes have not been investigated, although *Rhabditis spp.* are phoretic on dung beetles (Triffit & Oldham 1927; Kuhnelt 1976; Sudhaus 1981). Disruption, aeration and burial of dung by scarabaeids cause destruction of parasitic nematode eggs and subsequent reductions in nematode population density (Bornemissza 1960; Reinecke 1960; Bryan 1973, 1976; Fincher 1973, 1975; Bergstrom *et al.* 1976; English 1979). Insects may exert similar effects on bacteriophagous nematodes. Additionally, Miller (1961) showed that scarabaeid beetles cause destruction of nematode eggs as they feed.

Detritivorous arthropods distribute fungal spores, mycelial fragments, and bacteria in their feces and on their bodies. Litter arthropods inoculate freshly-fallen leaf litter with fungi from their feces which enhances litter breakdown (Engelmann 1961; Healey 1967). Parkinson *et al.* (1979) demonstrated that *Onychiurus subtenius* Folsom (Collembola) carries spores of various fungi on its body. Collembola can transport spores or mycelial fragments of as many as 130 separate fungal species (Hassal *et al.* 1983). Such transported microbes caused increased microbial respiration in microcosms of decomposing leaf litter (Visser *et al.* 1981). Similar effects occur in decomposing branchwood (Ausmus 1977) and leaf packs in woodland streams (Anderson *et al.* 1978).

Lussenhop *et al.* (1980) demonstrated that cow dung which was colonized normally by arthropods had greater number of fungal species than dung without insects. This finding, in conjunction with the evidence that grazing by larval flies reduces fungal species richness (Wicklow & Yocum 1982), suggests that arthropods are important in the dispersal of some coprophilous fungi.

5. Acknowledgements

We are grateful for the helpful comments provided by Drs. ROBERT L. BURGESS, NEIL H. RINGLER, MYRON J. MITCHELL and the anonymous reviewers who read the initial drafts of this paper.

6. References

ABRAMS, B. I., & M. J. MITCHELL, 1980a. Role of nematode-bacteria interactions in heterotrophic systems with emphasis on sewage sludge decomposition. Oikos **35**, 404—410.

— — 1980b. Interactions between nematodes and bacteria in heterotrophic systems with emphasis on sewage sludge and sludge-amended soils, pp. 583—591. *In:* D. L. DINDAL (ed.), Soil Biology as Related to Land Use Practices. USEPA, Washington, D.C.

ANDERSON, J. M., & D. E. BIGNELL, 1979. Bacteria in the food, guts and faeces of the millipede *Glomeris marginata* (VILLERS). Soil Biol Biochem. **12**, 251—254.

— & M. J. COE 1974. Decomposition of elephant dung in an arid, tropical environment. Oecologia (Berl.) **14**, 111—125.

— & P. INESON, 1983. Interactions between soil arthropods and microorganisms in carbon, nitrogen and mineral element fluxes from decomposing leaf litter, pp. 413—432. *In:* J. A. LEE, MCNEILL & I. R. RORISON (eds.), Nitrogen as an Ecological Factor. Blackwell Scientific Publications, Oxford.

— — & S. A. HUISH, 1983. The effects of animal feeding activities on element release from deciduous forest litter and soil organic matter, pp. 87—100. *In:* PH. LEBRUN, H. M. ANDRE, A. DE MEDTS, C. GREGOIRE-WIBO & G. WAUTHY (eds.), New Trends in Soil Biology. Proceedings of the VIII Intl. Colloquium of Soil Zoology, Dieu-Brichart, Ottignies-Louvain-la-Neuve.

ANDERSON, N. H., & J. R. SEDELL, 1979. Detritus processing by macroinvertebrates in stream ecosystems. Ann. Rev. Entomol. **24**, 351—377.

— — L. M. ROBERTS & F. J. TRISKA, 1978. The role of aquatic invertebrates in processing wood debris in coniferous forest streams. Amer. Midl. Nat. 100, 64—82.

ANDERSON, R. V., W. D. GOULD, L. E. WOODS, C. CAMBARDELLA, R. E. INGHAM & D. C. COLEMAN, 1983. Organic and inorganic nitrogenous losses by microbivorous nematodes in soil. Oikos **40**, 75—80.

AUSMUS, B. S., 1977. Regulation of wood decomposition rates by arthropod and annelid populations. Ecol. Bull. (Stockholm) **25**, 180—912.

— & M. WITKAMP, 1973. Litter and soil microbial dynamics in a deciduous forest stand. (EDFP-IBP-73-10) Oak Ridge Nat. Lab., Oak Ridge, TN.

BAKER, J. H., & L. A. BRADMAN, 1976. The roles of bacteria in the nutrition of aquatic detritivores. Oecologia (Berl.) **24**, 95—104.

BEAVER, R. A., 1977. Non-equilibrium 'island' communities: Diptera breeding in dead snails. J. Anim. Ecol. **46**, 783—798.

BENFIELD, E. F., D. S. JONES & M. F. PATTERSON, 1977. Leaf pack processing in a pastureland stream. Oikos **29**, 99—103.

BERGSTROM, R. C., L. R. MAKI & B. A. WERNER, 1976. Small dung beetles as biological control agents: laboratory studies of beetle action on trichostrongylid eggs in sheep and cattle feces. Proc. Helminth. Soc. Wash. **43**, 171—174.

BERTRAND, M., & J. P. LUMARET, 1984. Effects on microarthropod populations of the burial of sheep feces by scarabaeids under extreme climatic conditions. Pedobiologia **27**, 51—66.

BLUME, R. R., J. J. MATTER & J. L. ESCHLE, 1973. *Onthophagus gazella:* effect on survival of horn flies in laboratory. Environ. Entomol. **2**, 81—813.

BORNEMISSZA, G. F., 1960. Could dung-eating insects improve our pastures? J. Aust. Inst. Agric. Sci. **26**, 54—56.

— 1969. A new type of brood care observed in the dung beetle *Oniticellus cinctus* (Scarabaeidae). Pedobiologia **9**, 223—225.

— 1970. Insectory studies on the control of dung breeding flies by the activity of the dung beetle, *Onthophagus gazella* F. (Coleoptera: Scarabaeinae). J. Aust. Entomol. Soc. **9**, 31—41.

— & C. H. WILLIAMS, 1970. An effect of dung beetles on plant yield. Pedobiologia **10**, 1—7.

BREYMEYER, A., 1974. Analysis of a sheep pasture ecosystem in the Pieniny Mountains (the Carpathians). XI. The role of coprophagous beetles (Coleoptera, Scarabaeidae) in the utilization of sheep dung. Ekol. Pol. **22**, 617—634.

— H. JAKUBCZYK & E. OLECHOWICZ, 1975. Influence of coprophagous arthropods on microorganisms in sheep feces laboratory investigations. Bull. Acad. Pol. Sci. **23**, 257—262.

BROWN, B. A., & M. J. MITCHELL, 1981. Role of the earthworm, *Eisenia foetida*, in affecting survival of *Salmonella entiridia* ser. *typhimurium*. Pedobiologia **22**, 434—438.

— B. L. SWIFT & M. J. MITCHELL, 1978. The effect of *Oniscus asellus* feeding on bacterial and nematode populations of sewage sludge. Oikos **20**, 90—94.

BRYAN, R. P., 1973. The effects of dung beetle activity on the numbers of parasitic gastrointestinal helminth larvae recovered from pasture samples. Aust. J. Agric. Res. **24**, 161—168.
— 1976. The effect of the dung beetle, *Onthaphagus gazella*, on the ecology of the infective larvae of gastrointestinal nematodes. Aust. J. Agric. Res. 567—574.
BUNNELL, F. L., D. E. N. TAIT & P. W. FLANAGAN, 1977. Microbial respiration and substrate weight loss. II. A model of the influence of chemical composition. Soil Biol. Biochem. **9**, 41—47.
CHEW, R. M., 1974. Consumers as regulators of ecosystems: an alternative to energetics, Ohio J. Sci. 74, 359—370.
CORNABY, B. W., C. S. GIST & D. A. CROSSLEY, Jr., 1975. Resource partitioning in leaf litter faunas from hardwood converted to pine forests, pp. 588—597. *In:* F. G. HOWELL & M. H. SMITH (eds.), Mineral Cycling in Southeastern Ecosystems. ERDA Symp. Ser. (CONF. 740513). NTIS, Springfield, Va.
CROSSLEY, D. A., Jr., 1977. The role of terrestrial saprophagous arthropods in forest soils: current status of concepts, pp. 49—56. *In:* W. J. MATTSON (ed.), The Role of Arthropods in Forest Ecosystems. Springer-Verlag, New York.
CUMMINS, K. W., R. C. PETERSEN, F. O. HOWARD, J. C. WUYCHECK & V. I. HOLT, 1973. The utilization of leaf litter by stream detritivores. Ecology **54**, 336—345.
CURRY, J. P., 1976. Some effects of animal manures on earthworms in grassland. Pedobiologia **16**, 425—438.
D'AMATO, L. A., F. W. KNAPP & D. A. DAHLMAN, 1980. Survival of the face fly in feces from cattle fed alfalfa hay or grain diets: effect of fermentation and microbial changes. Environ. Entomol. **9**, 557—560.
DICKINSON, C. H., & V. H. S. UNDERHAY, 1977. Growth of fungi in cattle dung. Trans. Brit. Mycol. Soc. **69**, 473—478.
DINDAL, D. L., 1973. Microcommunities defined, pp. 2—6, *In:* D. L. DINDAL (ed.), Proceedings of the First Soil Microcommunities Conference. USAEC (CONF. 711076). NTIS, Springfield, Va.
— L. T. NEWELL & J. P. MOREAU, 1979. Municipal wastewater irrigation: effects on community ecology of soil invertebrates, pp. 197—205. *In:* W. E. SOPPER & S. N. KERR (eds.), Utilization of Municipal Sewage Effluent and Sludge on Forest and Disturbed Land. Pennsylvania State University Press, University Park.
DOWDING, V. M., 1967. The function and ecological significance of the pharyngeal ridges occurring in the larvae of some cyclorraphagous Diptera. Parasitology **57**, 371—388.
DRIFT, J. VAN DER & E. HANSEN, 1977. The grazing of springtails on hyphal mats and its influence on fungal growth and respiration. Ecol. Bull. (Stockholm) **25**, 203—209.
— & M, WITKAMP, 1960. The significance of the breakdown of oak litter by *Enoicyla pusilla* BURM. Arch. Neerl. Zool. **13**, 486—492.
EDWARDS, C. A., D. E. REICHLE & D. A. CROSSLEY, Jr., 1970. The role of soil invertebrates in turnover of organic matter and nutrients, pp. 147—172. *In:* D. E. REICHLE (ed.), Analysis of Temperate Forest Ecosystems. Ecological Studies 1. Springer-Verlag, New York.
EDWARDS, R. W., 1958. The effect of larval *Chironomus riparius* MEIGEN on the redox potential of settled activated sewage sludge. Ann. Appl. Biol. **46**, 457—464.
— & H. L. J. ROLLEY, 1965. Oxygen consumption of river muds. J. Ecol. **53**, 1—19.
ENGELMANN, M. D., 1961. The role of soil arthropods in the energetics of an old field community. Ecol. Monogr. **31**, 221—238.
ENGLISH, A. W., 1979. The effects of dung beetles (Coleoptera: Scarabaeinae) on the free-living stages of strongylid nematodes of the horse. Aust. Vet. J. **55**, 315—321.
FAY, H. A. C., & B. M. DOUBE, 1983. The effects of some coprophagous and predatory beetles on the survival of immature stages of the African buffalo fly, *Haematobia thirouxi potans*, in bovine dung. Z. Angew. Entomol. **95**, 460—466.
FENCHEL, T., & P. HARRISON, 1976. The significance of bacterial grazing and mineral cycling for the decomposition of particulate detritus, pp. 285—299. *In:* J. M. ANDERSON & A. MACFADYEN (ed.), The Role of Terrestrial and Aquatic Organisms in Decomposition Processes, Blackwell Scientific Publications, Oxford.
FERRAR, P., 1975. Preamble for symposium on effects of dung beetles, J. Appl. Ecol. **12**, 819—821.
FINCHER, G. T., 1973. Dung beetles as biological control agents for gastrointestinal parasites of livestock. J. Parasit. **59**, 396—399.
— 1975. Effects of dung beetle activity on the number of nematode parasites aquired by grazing cattle. J. Parasit. **61**, 759—762.
— 1981. The potential value of dung beetles in pasture ecosystems. J. Georgia Entomol. Soc. **16**, 316—333.
— W. G. NONSON & G. W. BURTON, 1981. Effects of cattle feces rapidly buried by dung beetles on yield and quality of coastal burmudagrass. Agron J. **73**, 775—779.
GILLARD, P., 1967. Coprophagous beetles in pasture ecosystems. J. Aust. Inst. Agric. Sci. **33**, 30—34.
GOODEY, T., 1963. Soil and freshwater nematodes. Methuen, London, 544 pp.
GRAY, T. R. G., & S. T. WILLIAMS, 1971. Soil Micro-organisms. Longman Group, Ltd., London 240 pp.
HALFFTER, G., & E. G. MATTHEWS, 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). Folia Entomol. Mexicana 12—14, 1—312.

— — 1971. The natural history of dung beetles: a supplement on associated biota. Rev. Lat.-Amer. Microbiol. **13**, 147—167.

HANLON, R. D. G., &. J. M. ANDERSON, 1979. The effects of collembolan grazing on microbial activity in decomposing leaf litter. Oecologia (Berl.) **38**, 93—99.

— — 1980. Influence of macroarthropod feeding activities on microflora in decomposing oak leaves. Soil Biol. Biochem. **21**, 255—261.

HARGRAVE, B. T., 1970. The effect of a deposit-feeding amphipod on the metabolism of benthic microflora. Limnol. Oceanogr. **15**, 21—30.

— 1976. Invertebrate feaces in sediments, pp. 301—321. *In:* J. M. ANDERSON & A. MACFADYEN (eds.), The Role of Terrestrial and Aquatic Organisms in Decomposition Processes. Blackwell Scientific Publications, Oxford.

HARTENSTEIN, R., 1982. Soil macroinvertebrates, aldehyde oxidase, catalase, cellulase and peroxidase. Soil Biol. Biochem. **14**, 387—391.

HASSAL, M., D. PARKINSON & S. VISSER, 1983. The effects of *Onychiurus subtenuis* on the microbial decomposition of *Populus tremuloides* leaf litter, p. 613. *In:* PH. LEBRUN ,H. M. ANDRÉ, A. DE MEDTS, C. GRÉGOIRE-WIBO & G. WAUTHY (eds.), New Trends in Soil Zoology, Proceedings of the VIII Intl. Colloquium of Soil Zoology, Dieu-Brichart, Ottignies-Louvain-la-Neuve.

HATA, K., & W. D. EDMONDS, 1983. Structure and function of the mandibles of adult dung beetles (Coleoptera: Scarabaeidae). Int. J. Insect Morphol. Embryol. **12**, 1—12.

HEALEY, I. N., 1967. The energy flow through a population of soil Collembola, pp. 695—708. *In:* K. PETRUSEWICZ (ed.), Secondary Productivity of terrestrial Ecosystems. Pol. Acad. Sci., Warsaw.

HOLTER, P., 1974. Food utilization of dung-eating *Aphodius* larvae (Scarabaeidae). Oikos **25**, 75—79.

— 1975. Energy budgets of a natural population of *Aphodius* larvae (Scarabaeidae). Oikos **26**, 177to 186.

— 1977. An experiment on dung removal by *Aphodius* larvae (Scarabaeidae) and earthworms. Oikos **28**, 130—136.

— 1979a. Abundance and reproductive strategy of the dung beetle, *Aphodius rufipes* (L.) (Scarabaeidae). Ecol. Entomol. **4** 317—326.

— 1979b. Effect of dung beetles (*Aphodius spp.*) and earthworms on the disappearance of cattle dung. Oikos **32**, 393—402.

HORNOR, S. G., & M. J. MITCHELL, 1981. Effect of the earthworm, *Eisenia foetida* (Oligochaeta), on fluxes of volatile carbon and sulfur compounds from sewage sludge. Soil Biol. Biochem. **13**, 367—372.

HUNT, H. W., 1977. A simulation model for decomposition in grassland. Ecology **58**, 469—484.

HUGHES, R. D., 1975. Assessment of the burial of cattle dung by Australian dung beetles. J. Aust. Entomol. Soc. **14**, 129—134.

— M. TYNDALE-BISCOE & J. WALKER, 1978. Effects of introduced dung beetles (Coleoptera: Scarabaeidae) on the breeding and abundance of the Australian bushfly *Musca vetustissima* WALKER (Diptera: Muscidae). Bull. Entomol. Res. **68**, 361—372.

INESON, P., M. A. LEONARD & J. M. ANDERSON, 1982. Effects of collembolan grazing upon nitrogen and cation leaching from decomposing leaf litter. Soil Biol. Biochem. **14**, 601—605.

KIRK, A. A., 1983. The biology of *Bubas bison* (Coleoptera: Scarabaeidae) on southern France and its potential for recycling dung in Australia. Bull. Entomol. Res. **73**, 129—136.

KOWAL, N. E., & D. A. CROSSLEY, Jr., 1971. The ingestion rates of microarthropods in pine mor, estimated with radioactive calcium. Ecology **52**, 444—452.

KÜHNELT, W., 1976. Soil biology, with special reference to the animal kingdom, second edition. Faber and Faber, London. 483 pp.

KURCHEVA, G. F., 1960. The role of invertebrates in the decomposition of oak leaf litter. Pocvovedenie 4, 16—23.

LANDIN, B.-O., 1961. Ecological studies on dung beetles (Coleoptera: Scarabaeidae). Opusc. Entomol., Suppl. **19**, 1—227.

LAVELLE, P., Z. ZAIDE & R. SCHAEFFER, 1983. Interactions between earthworms, soil organic matter, and microflora in an African savanna soil, pp. 253—259. *In:* PH. LEBRUN, H. M. ANDRÉ, A. DE MEDTS, C. GRÉGOIRE-WIBO & G. WAUTHY (eds.), New Trends in Soil Biology. Proceedings. of the VIII Intnl. Colloquium of Soil Zoology. Dieu-Brichart, Ottignies-Louvain-la-Neuve.

LEVINGTON, J. S., & G. R. LOPEZ, 1977. A model of renewable resources and limitation of deposit-feeding benthic populations. Oecologia (Berl.) **31**, 177—190.

LUSSENHOP, J., R. KUMAR, D. T. WICKLOW & J. E. LLOYD, 1980. Insect effects on bacteria and fungi in cattle dung. Oikos **34**, 54—58.

MACFAYDEN, A., 1961. Metabolism of soil invertebrates in relation to soil fertility. Ann. Appl. Biol. **49**, 215—218.

MACLEAN, S. F., Jr., 1974. Primary production, decomposition, and the activity of soil invertebrates in tundra ecosystems: a hypothesis, pp. 197—206. *In:* A. J. HOLDING (ed.), Soil Organisms and Decomposition in Tundra.

MacQueen, A., & B. P. Beirne, 1975a. Dung burial activity and fly control potential of *Onthophagus nuchicornis* (Coleoptera: Scarabaeinae) in British Columbia. Canad. Entomol. **107**, 1215 to 1220.
— — 1975b. Influence of some dipterous larvae on nitrogen loss from cattle dung. Environ. Entomol. **4**, 868—870.
Madle, H., 1934. Zur Kenntnis der Morphologie, Ökologie und Physiologie von *Aphodius rufipes* L. und einigen verwandten Arten. Zool. Jb. Abt. Anat. **58**, 303—396.
Mason, W. H., & E. P. Odum, 1969. The effects of coprophagy on retention and bioelimination of radionucleotides by detritus-feeding animals, pp. 721—724. *In:* D. J. Nelson & F. C. Evans (eds.), Symposium on Radioecology. USAEC (CONF 607503). NTIS, Springfield, Va.
Matthiessen, J. N., L. Hayes & M. J. Palmer, 1984. An assessment of some methods for the bioassay of changes in cattle dung as insect food, using the bushfly. *Musca vetustissima* (Diptera: Muscidae). Bul. Entomol. Res. **74**, 463—467.
McBrayer, J. F., 1973. Exploitation of deciduous leaf litter by *Apheloria montana* (Diplopoda: Eurydesmidae). Pedobiologia **13**, 90—98.
— & D. E. Reichle, 1971. Trophic structure and feeding rate of forest soil invertebrate populations Oikos **22**, 381—388.
— — & M. Witkamp, 1974. Energy flow and nutrient cycling in a cryptozoan food-web. (EDFB-IBP-74-8). Oak Ridge Natl. Lab., Oak Ridge, Tenn.
McKinney, G. T., & F. H. W. Morley, 1975. The agronomic role of introduced dung beetles in grazing systems. J. Appl. Ecol. **12**, 831—837.
Merritt, R. W., 1974. The species diversity and abundance of insects inhabiting cattle droppings and their role in the degradation of dung in four contrasting pasture and rangeland ecosystems in the Sierra Nevada foothills of California. Ph. D. Dissertation, Univ. Calif., Berkeley, Calif. 237 pp.
Miller, A., 1961. The mouthparts and digestive tract of adult dung beetles (Coleoptera: Scarabaeidae), with reference to the ingestion of helminth eggs. J. Parasit. **47**, 735—744.
Minderman, G., 1968. Addition, decomposition, and accumulation of organic matter in forests. J. Ecol. **56**, 355—362.
Mitchell, M. J., 1979. Functional relationships of macroinvertebrates in heterotrophic systems with emphasis on sewage sludge decomposition. Ecology **60**, 1270—1283.
— R. Hartenstein, B. L. Swift, E. F. Neuhauser, B. I. Abrams, R. M. Mulligan, B. A. Brown, D. Graig & D. L. Kaplan, 1978. Effects of different sewage sludges on some chemical and biological characteristics of soil. J. Environ. Qual. **9**, 373—378.
— S. G. Hornor & B. I. Abrams, 1980. Decomposition of sewage sludge in drying beds and the potential role of the earthworm, *Eisenia foetida*. J. Environ. Qual. **9**, 373—378.
Mulholland, P. J., J. W. Elwood, J. D. Newbold & L. A. Ferran, 1985. Effect of a leaf shredding invertebrate on organic matter dynamics and phosphorus spiralling in heterotrophic laboratory streams. Oecologia (Berl.) **66**, 199—206.
Myrcha, A., 1973. Bioenergetics of the developmental period of *Copris lunaris* L. Ekol. Pol. **21**, 13—25.
Nakamura, Y., 1975. Role of dung beetles in the decay of cow dung. Bull. Natl. Grassl. Inst. **7**, 48 to 51.
Newell, K., 1984. Interaction between two decomposer basidiomycetes and a collembolan under Sitka spruce: grazing and its potential effects on fungal distribution and litter decomposition. Soil. Biol. Biochem. **16**, 235—239.
Nicholson, P. B., K. L. Bocock & O. W. Heal, 1966. Studies on the decomposition of faecal pellets of millipede [*Glomeris marginata* (Villers)]. J. Ecol. **54**, 755—766.
Olechowicz, E., 1976. The role of coprophagous dipterans in a mountain pasture ecosystem. Ekol. Pol. **24**, 125—165.
Olson, J. S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology **44**, 322—331.
Omaliko, C. P. E., 1981. Dung deposition, breakdown and grazing behaviour of beef cattle at two seasons in a tropical grassland ecosystem. J. Range Managem. **34**, 360—362.
Overgaard-Nielsen, C., 1962. Carbohydrases in soil and litter invertebrates. Oikos **13**, 200—215.
Parker, L. W., P. F. Santos, J. Phillips & W. G. Whitford, 1984. Carbon and nitrogen dynla during the decomposition of litter and roots of a Chihuahuan desert annual, *Lepidium lasiocarpum*. Ecol. Monogr. **54**, 339—360.
Parkinson, D., 1983. Functional relationships between soil organisms, pp. 153—165. *In:* Ph. Lebrun, H. M. André, A. De Medts, C. Grégoire-Wibo & G. Wauthy (eds.), New Trends in Soil Biology. Proceedings of the VIII Intnl. Calloquium of Soil Zoology. Dieu-Brichart, Ottignies-Louvain-la-Neuve.
— S. Visser & J. B. Whittaker, 1979. Effects of collembolan grazing on fungal colonization of leaf litter. Soil. Biol. Biochem. **11**, 529—535.
Parle, J. N., 1963. Microogranisms in the intestines of earthworms. J. Gen. Microbiol. **31**, 1—11.
Petersen, H., & Luxton, 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos **39**, 287—388.

REINECKE, P. K., 1960. A field study of some nematode parasites of bovines and possible methods of prophylaxis. Onderstepoort. J. Vet. Res. **28**, 103—108.
REYES, V. G., & J. M. TIEDJE, 1975. Metabolism of the C^{14}-labelled plant materials by woodlice (*Tracheoniscus rathkei* BRANDT) and soil organisms. Soil Biol. Biochem. **8**, 102—108.
RIDSDILL SMITH, T. J., G. P. HALL & G. F. CRAIG, 1982. Effect of population density on reproduction and dung dispersal by the dung beetle, *Onthaphagus binodus*, in the laboratory. Entomol. Exp. Agric. **32**, 80—85.
SATCHELL, J. E., & K. MARTIN, 1984. Phosphatase activity in earthworm faeces. Soil Biol. Biochem. **16**, 191—194.
SEADSTEDT, T. R., 1984. The role of microarthropods in decomposition and mineralization processes. Ann. Rev. Entomol. **29**, 24—46.
SHORT, R. A., & P. E. MASLIN, 1977. Processing of leaf litter by a stream detritivore: effect on nutrient availability to collectors. Ecology **58**, 935—938.
SMITH, T. J. R., 1981. Some effects of three species of dung beetles (Coleoptera: Scarabaeidae) in southwestern Australia on the survival of the bushfly, *Musca vetustissima* WALKER (Diptera: Muscidae), in dung pads. Bull. Entonomol. Res. **71**, 425—433.
STEFANIAK, O., & S. SENICAK, 1976. The microflora of the alimentary canal of *Achiptera coleoptera* (Acarina, Oribatei). Pedobiologia **16**, 185—194.
STEVENSON, B. G., & D. L. DINDAL, 1987. Insect effects on decomposition of cow dung in microcosms. Pedobiologia. **30**, 73—80.
— C. M. PARKINSON & M. J. MITCHELL, 1984. Effect of sewage sludge on decomposition proceses in soil. Pedobiologia **26**, 95—105.
STOUT, J. D., 1973. The relationship between protozoan populations and biological activity in soils. Amer. Zool. **13**, 193—201.
SZABO, I., M. MARTON & I. BUTI, 1969. Intestinal microflora of St. Mark's fly. IV. Studies on the intestinal bacterial flora of the larval population. Acta Microbiol. Acad. Scient. Hungaricae **16**, 381—397.
TRIFFIT, M. J., & H. N. OLDHAM, 1927. Observations on the morphology and bionomics of *Rhabdilis coartata* LEUCK., **5**, 33—46.
VISSER, S., J. B. WHITTAKER & D. PARKINSON, 1981. Effects of collembolan grazing on nutrient release and respiration of a leaf litter inhabiting fungus. Soil Biol. Biochem. **13**, 215—218.
WALLACE, M. M. H., & M. TYNDALE-BISCOE, 1983. Attempts to measure the influence of dung beetles (Coleoptera: Scarabaeidae) on the field mortality of the bush fly. *Musca vetustissima* (Diptera: Muscidae) in southeastern Australia. Bull. Entomol. Res. **73**, 33—44.
WALLWORK, J. A., 1983. Oribatids in forest ecosystems. Ann. Rev. Entomol. **28**, 109—130.
WEBB, D. P., 1977. Regulation of deciduous forest litter decomposition by soil arthropod feces, pp. 57—69. *In:* W. J. MATTSON (ed.), The Role of Arthropods in Forest Ecosystems. Springer-Verlag, New York.
WENT, J. C., 1963. Influence of some earthworms on the number of bacteria in the soil, pp. 260—265. *In:* J. DOEKSON & J. VAN DER DRIFT (eds.), Soil Organisms. North Holland Press, Amsterdam.
WHITFORD, W. G., Y. STEINBERGER & G. ETTERSHANK, 1982. Contributions of subterranean termites to the economy of Chihuahuan desert ecosystems. Oecologia (Berl.) **55**, 298—302.
— D. W. FRECKMAN, L. W. PARKER, D. SCHAEFFER, P. F. SANTOS & Y. STEINBERGER, 1983. The contribution of soil fauna to nutrient cycles in desert ecosystems, pp. 49—57. *In:* PH. LEBRUN, H. M. ANDRÉ, A. DE MEDTS, C. GRÉGOIRE-WIBO & G. WAUTHY (eds.), New Trends in Soil Biology. Proceedings of the VIII Intnl. Colloquium of Soil Zoology. Dieu-Brichart, Ottignies-Louvain-la-Neuve.
WICKLOW, D. T., R. KUMAR & J. E. LLOYD, 1984. Germination of blue grama seeds buried by dung beetles (Coleoptera: Scarabaeidae). Environ. Entomol. **13**, 878—881.
— & D. H. YOCUM, 1982. Effect of larval grazing by *Lycoriella mali* (Diptera: Sciaridae) on species abundance of coprophilous fungi. Trans. Brit. Mycol. Soc. **78**, 29—32.
WITKAMP, M., & D. A. CROSSLEY, Jr., 1966. The role of arthropods and microflora in breakdown of white oak litter. Pedobiologia **6**, 293—303.

Address of the authors: B. G. STEVENSON (corresponding author) and D. L. DINDAL, Department of Environmental and Forest Biology, State University of New York, College of Environmental Science and Forestry, Syracuse, New York 13210, USA.

Synopsis: *Subject review article*

STEVENSON, G. B., & D. L. DINDAL, 1987. Functional ecology of coprophagous insects: A review. Pedobiologia **30**, 285—298.

Coprophagous arthropods actively contribute to the degradation of fecal material, particularly ruminant dung. Most research on coprophagous arthropods has dealt with their beneficial activity in the maintenance and utilization of agricultural ecosystems. The purpose of this paper is to examine (a total of 137 references has been included) the roles of these organisms in the context of consumer regulation of organic matter decomposition. Since the majority of related research has focused on ruminant dung, this review emphasizes the roles of invertebrates inhabiting it.

Dung arthropods exhibit many of the same characteristics of other detrivorous invertebrates. They aerate dung and promote aerobic decomposition through interactions with microflora, including formation of invertebrate feces. The extent to which these organisms actually contribute to dung degradation depends upon their population density and micro-environmental factors such as dung moisture and temperature, and upon the distribution of dung which is a function of the distribution and stocking density of livestock.

Key words: Coprophagous insects, functional interactions, consumer regulation, ruminant dung, degradation of feces, microbial and zootic metabolism, decomposition processes, population density, livestock, stocking density.

Pedobiologia.
Verlag: VEB Verlage für Medizin und Biologie Berlin-Jena-Leipzig, VEB Gustav Fischer Verlag Jena, Villengang 2, Jena, DDR - 6900 ; Telefon 27332.
Verantwortlich für die Redaktion: Dr. E. von Törne, Rudolf-Breitscheid-Straße 48, Eberswalde-Finow 1, DDR - 1300.
Redaktioneller Mitarbeiter im Verlag: Carola Köber.
Veröffentlicht unter der Lizenznummer 1074 des Presseamtes beim Vorsitzenden des Ministerrates der Deutschen Demokratischen Republik.
Redaktionsschluß der Karte: Dezember 1986 (Cox/Gakahu)
Satz, Druck und Buchbinderei: Druckerei „Magnus Poser" Jena, Betrieb des Graphischen Großbetriebes INTERDRUCK Leipzig, Betrieb der ausgezeichneten Qualitätsarbeit.
Alle Rechte beim Verlag, Nachdruck (auch auszugsweise) mit Ausnahme der Synopsen nur mit Genehmigung des Verlages und des Verfassers sowie mit Quellenangabe gestattet.
Printed in the German Democratic Republic.
Artikel-Nr. (EDV) 66215; Artikel-Nr. (ZV) 111 800 2633.
Erscheinungsweise: 6mal jährlich
01870